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Habitat requirements of the horned lizard Phrynosoma mcallii in a disturbed desert environment

Bernard Wone
San Jose State University

Order Number 1348731

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Wone, Bernard, M.A.

San Jose State University, 1992

U·M·I
300 N. Zeeb Rd.
Ann Arbor, MI 48106

HABITAT REQUIREMENTS OF THE HORNED LIZARD

PHRYNOSOMA MCALLII

IN A DISTURBED DESERT ENVIRONMENT

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Bernard Wone

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APPROVED FOR THE DEPARTMENT OF BIOLOGICAL SCIENCES

William E Bros

Dr. William Bros

Michael Kutilek

Dr. Michael Kutilek

Howard Shellhammer

Dr. Howard Shellhammer

APPROVED FOR THE UNIVERSITY

Serena W. Stanford

ABSTRACT

HABITAT REQUIREMENTS OF THE HORNED LIZARD

PHRYNOSOMA MCALLII

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by Bernard Wone

The relationship between habitat features and both lizard and scat occurrence was investigated for *Phrynosoma mcallii*. The population of *P. mcallii* studied within Ocotillo Wells State Vehicle Recreation Area and the adjoining acquisition area was negatively correlated to the presence of their scats ($r = -0.775$). Further, cover and substrate were found to be important habitat features that affect the distribution of *P. mcallii*. Of the two factors extracted from Principal Components Analysis, Factor 2 was the significant descriptor indicating that *P. mcallii* were associated with bare ground covered with small pebbles/gravel in between sparse cover, while their scats were associated with much cover by vegetation and rocks. Significant differences between lizard and scat locations indicated daily shifts in microhabitat use by this species. Results from this study elucidated some habitat requirements for *P. mcallii* but it is not enough to provide a meaningful conservation plan for the species.

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INTRODUCTION

There is little available information on the habitat requirements of the horned lizard Phrynosoma mcallii. Previous habitat information contained only qualitative descriptions of features where P. mcallii occurred. Turner et al. (1980) reported that the best P. mcallii "habitats generally have surface soils of finely packed sand or desert pavement overlain intermittently with loose fine sand." Others have associated P. mcallii with areas containing aeolian sand hummocks interspersed with creosote bush (Norris, 1949), areas covered with small pebbles or gravel areas located near sandy areas (Turner et al., 1980), extremely barren with sparse or no vegetation, and sharing the same habitat as the fringe-toed lizard (Stebbins, 1985).

Information on the habitat requirements of an organism is essential when proposing and testing hypotheses. Habitat requirements of lizards are often described in the context of habitat use and are probably the most studied aspect (Schoener, 1977). These uses are often described in terms of lizard's response to a thermal environment (Porter et al,. 1973; Porter and James, 1979; Waldschmidt and Tracy, 1983; Grant and Dunham, 1988; Medel et al.. 1988; Law and Bradely, 1990; Adolph 1990b), to interspecfic competition and resource partitioning (Heatwole, 1977; Schoener, 1977; Gonzalez-Romero and Barbault, 1989; Baltosser and Best, 1990; Shenbrot et al., 1991; Stamps, 1991), while some described habitat use in the context of reproduction (Huey, 1982; M'Closkey et al., 1989).

Data on habitat requirements of an organism are needed to develop conservation plans for endangered species and proper management of their habitats (Heggenes, 1989; Bright and Morris, 1990). The conservation and management of endangered lizard habitats are probably the most important aspect of reptile conservation (Rawlinson, 1981). Presently, Phrynosoma mcallii is listed as a candidate for endangered status by the U. S. Fish and Wildlife Service and is a California Species of Special Concern. It may be difficult to conserve because its habitats are becoming increasingly fragmented as a result of human activities (Turner and Medica, 1982; England, 1983; Bolster and Nicol, 1989). Furthermore, the small amount of biological, ecological, and habitat information currently available is not enough to determine preserve size and quality necessary to maintain minimum viable populations (Bolster and Nicol, 1989).

Because of the small amount of habitat data available on P. mcallii, previous information is misleading. Turner and Medica (1982) reported "the relative abundance of P. mcallii was significantly and positively correlated with aggregate perennial density." This is not a correct statement because Turner and Medica (1982) used a relative abundance index based on lizard and scat counts as the dependent variable in their stepwise multiple regression. Of the ten plots used in their study, only 4 P. mcallii were counted, which means the abundance index was calculated from scat. Therefore, their results can be interpreted as P. mcallii scat abundance being positively correlated to aggregate perennial density. The relative abundance index also was used as a measure of abundance, distribution, and habitat quality for P. mcallii in California and Arizona (Turner and Medica, 1982; Rorabaugh et al., 1987). Because low numbers of P. mcallii were often observed during surveys (Turner et al., 1980; Klinger et al., 1990; Wone et al., 1991), the abundance index was really based on scats counts. Furthermore, the abundance estimate technique also assumed that the number of P. mcallii was directly proportional to the number of scats observed (Olech, 1984). At present, the United States Department of Interior, Bureau of Land Management and California

Department of Fish and Game are using the relative abundance index as a indicator of lizard abundance, distribution and habitat use in various areas (Bolster and Nicol, 1989). The use of scats as an indicator may be misleading because the relationship between the lizards and the presence of their scats is unknown. If meaningful P. mcallii conservation plans are to be developed, a basic knowledge of its habitat requirements needs to be established.

In this study I examined the relationship between habitat features and both lizard and scat presence for the horned lizard P. mcallii. I investigated the relationship between lizards and their scats. Secondly, I compared habitat diversity between the two locations to determine if the variety of land forms and plant life forms alone is sufficient to reveal their habitat requirements. Then, I explored how habitat features influenced lizard occurrence. These features (horizontal coverage, distance to nearest cover, and density of active harvester ant mounds) were examined on the premise that P. mcallii respond to aspects of substrate, cover and food availability in their environment. I also quantified differences between locations and then examined the effect of both lizard and scat presence on these differences. Finally, I evaluated possible reasons for the results and discussed the relevance of the findings to the conservation of this candidate endangered species.

THE ORGANISM

The horned lizard Phrynosoma mcallii is a myrmecophagous iguanid that occurs disjunctively in the deserts of southeastern California to southwestern Arizona and adjacent areas of Baja California and Sonora, Mexico (Funk, 1981; Stebbins, 1985;

Johnson, 1989). The species is more thermophilic than other phrynosomids (Heath, 1965) and is easily identified by a dark middorsal stripe with a very much flattened tail (Stebbins, 1985). Unlike its congeners, P. mcallii runs with great speed and is often mistaken for fringe-toed lizards when fleeing. Males are similar to other male iguanids in having enlarged postanal scales and a swollen tail base when breeding (Stebbins, 1985). They are generally found below sea level to approximately +180 m (Stebbins, 1985), but they have been collected at an elevation of 520 m (Turner et al., 1980).

STUDY AREA

Ocotillo Wells State Vehicular Recreation Area (SVRA) and the adjoining acquisition area are located in the Colorado Desert province 144 km northeast of San Diego on the boundary of San Diego and Imperial Counties, California (California Department of Parks and Recreation, 1981). Ocotillo Wells SVRA, 5,836 ha in size, lies on the plains east of the Borrego Mountains and is bordered on the north and west by Anza-Borrego Desert State Park. The acquisition area, 7272 ha in size, is contiguous with the eastern boundary of the SVRA and extends eastward to Pole Line Road. Both areas are bordered on the south by State Highway 78. Turner and Medica (1982) reported that areas located north of State Highway 78 in the vicinity of Ocotillo Wells were some of the most favorable for Phrynosoma mcallii.

Ocotillo Wells SVRA is 1 of 7 State Vehicular Recreation Areas maintained by the Off-Highway Motor Vehicular Recreation Division of the California Department of Parks and Recreation. The major use of the areas by Off-Highway Vehicle (OHV) riders is concentrated in the southern half of the SVRA and the acquisition area during the cooler months of the year.

Varied climates occur in the study area largely because Ocotillo Wells SVRA and the acquisition area are located in the rainshadow of the Peninsular Ranges. Intermittent moderate winds in the spring and summer are from the northwest and in the fall from the northeast. Winds in the fall and winter are often strong and can exceed speeds of 64 km/hr. Daily temperature range varies considerably throughout much of the year; during the summer months daytime temperatures usually exceed 38^{o} C with night time lows of 20^{o} C, while the winter daytime temperature is typically 20^{o} C and night time lows below 0^{o} C are common.

Topographically, Ocotillo Wells SVRA is flat with some areas of mudhills, moderately-rugged hills and dune systems. The acquisition area is also generally flat, but has extensive rugged mudhills. The elevation of Ocotillo Wells SVRA ranges from 40 m to 240 m. Both areas are interlaced by numerous washes; 8 of these are major ones, all of which are flooded during heavy rains.

The principal vegetation formation consists of creosote bush scrub (Larrea tridentata), saltbush (Atriplex sp.) and wash woodland communities. Other major plants within Ocotillo Wells SVRA include Franseri dumosa, Atriplex canescens, A. hymenelytra, A. ploycarpa, Hilaria ridgida, Eriogonum inflatum, E. deserticola, Dalea emoryi, D. shotii, Krameria grayi, Hyemnoclea salsola, Encelia farinosa, E. frutescens, Opuntia echinocarpa, Saudea fruticosa, Fouquieria splendens, Petalonyx thurberia Eriastrum densifiolium, and Coldenia palmeri (Kutilek et al., 1991). The spaces between perennials are generally bare, except after winter rains when a diversity of annuals may develop.

METHODS

Lizards and scats were counted to determine the degree to which P. mcallii is correlated with the presence of their scats. These data provided the number of lizards and/or scats at each location. The relationship between lizards and scats was examined using the Pearson correlation (Sokal and Rolf, 1981).

I measured horizontal coverage, distance to the nearest cover, and density of harvester ant mounds to determine how these variables influence lizard and scat presence. In addition three variables were calculated: sum of the patches of each horizontal feature, horizontal feature evenness and richness calculated from horizontal percent coverage, horizontal diversity calculated from horizontal percent coverage using the Shannon-Wiener formula (Brower and Zar, 1984). Because of the small sample size of active harvester ant mounds, the total density of all genera of harvester ant mounds were pooled for each location. These data provided habitat diversity, habitat richness and evenness, number and percent coverage of habitat features, the mean distance to the nearest available cover, and the density of active harvester ant mounds (no./1257 m^2) for each location. Prior to analyses, percentage data were transformed with the arcsin of the square root and data with positive skewness were transformed with log (x+1) to improve normality. All analyses were performed using Systat®, a statistical software package. Habitat diversity indexes, richness, and evenness were grouped for lizard or scat locations and analyzed by t-tests (Brower and Zar, 1984).

Hotelling's T^2 test was used to examine the main effect of lizard occurrence (presence and absence) on the variables describing the habitat (e. g. percent cover, mean distance to nearest available cover, etc.) of the locations. Hotelling's T^2 test is a special case of multivariate analysis of variance designed to test for differences between two groups when there is only one independent variable with two levels (Tabachnick and Fidell, 1989). Of the 19 habitat variables measured, only 9 were used in the analysis because of missing data and multicollinearity (Table 1). I performed a stepdown analysis (Tabachnick and Fidell, 1989) to investigate the impact of main effect on the individual variables. All habitat variables used in the Hotelling's T^2 test warranted stepdown analysis; therefore, each variable was analyzed with higher-priority variables treated as covariates (a series of ANCOVAs were performed). The highest-priority variable was tested with a one-way ANOVA. The assumptions for ANOVA were met.

Principal Component Analysis (PCA) (Tabachnick and Fidell, 1989) was used to account for and quantify differences between lizard and scat locations. PCA combined the habitat variables into a set of habitat descriptors (factors) which may reflect patterns of habitat variations. Important habitat components revealed by the stepdown analysis were used in PCA (Table 1). Only factors with eigenvalues >1.0 were retained for interpretation. Factors were interpreted by describing the ratio of variables with positive loadings to those with negative values.

Differences, in locations as quantitatively characterized by PCA, were analyzed by t-tests (Zar, 1984 for t-test) to reveal significant patterns of habitat characters for both lizard and scat occurrence in which hypotheses can be generated about Phrynosoma mcallii habitat requirements. Factor scores for each location were generated from the PCA factor coefficient matrix and were grouped for each type of location.

Table 1. Habitat features sampled at Ocotillo Wells State Vehicular Recreation Area and the Acquisition Area, June 1991. These variables were prioritized on the ecological importance to P. mcallii and were used in the Hotelling's T^2 test and stepdown analysis. Variables used in the Principal Components Analysis are starred.

Acronym	Habitat Feature
HVANT	Density of active harvester ant mounds (no./1257 m^2) at each location
NVEG*	Number of patches of vegetation at each location
NSAND	Number of patches of sand at each location
%DUNE	Percent of location covered by accretion dunes
%BARE*	Percent of location covered by bare ground
%GRAV*	Percent of location covered by small pebbles or gravel
NTRAIL	Number of patches of trail or wash at each location
MNDIST*	Mean distance to nearest cover
NROCK*	Number of patches of rocks at each location

Sampling of habitat features was done at 18 flagged P. mcallii capture/release locations, and at 13 locations where large numbers of their scats were observed during the P. mcallii surveys at Ocotillo Wells SVRA and the acquisition area (Wone et al., 1991). A total of 31 locations were sampled during June 1991. At each of the locations, 20-m tapes were placed perpendicular to the lizard survey transect on each side. Horizontal coverage was sampled by the line intercept method (Brower and Zar, 1984). The length of line intercepted by each species of vegetation, rock and type of substrate (e. g. bare ground, desert pavement, etc.) was recorded to the nearest centimeter. The nearest available cover was sampled by the nearest-neighbor method (Mueller-Dombois and Ellenberg, 1974). I measured the distance to the nearest shrub or patch of vegetation on each side of the tape from the start and end points of each 20-m line. P. mcallii scats and active harvester ant mounds were counted in a 20-m radius around the flagged location. Whenever possible, harvester ant mounds were identified to the species level.

RESULTS

Phrynosoma mcallii was inversely correlated to the presence of their scats (r = -0.775). Scats were rarely found near the vicinity where a lizard was captured and released. Moreover, P. mcallii were often found just out in the peripheral areas where large numbers of their scats were observed. Because scats were inversely correlated with lizards, I was unable to use the two variables simultaneously as independent variables in a canonical correlation.

The proportion and variety of land forms (e. g. rocks), type of substrate, and vegetation forms were not significantly different between locations with lizards or with scats ($p = 0.394$). Habitat diversity indexes of lizard locations ranged from 0.137 to 1.678, while scat locations ranged from -0.553 to 1.757. The minimum detectable difference for habitat diversity indexes was 0.737. Furthermore, t-tests indicated that richness and evenness of horizontal features between lizard and scat locations do not differ significantly ($p = 0.455$ and $p = 0.470$, respectively).

The type of substrate and cover had an effect on adult P. mcallii occurrence. Occurrence varied significantly as a function of different habitat features ($F = 3.63$, df = 9, 12, $p = 0.006$). The Hotelling's T^2 test also indicated that lizard occurrence was positively associated with the number of patches of vegetation and percentage of bare ground with a decrease in the mean distance to nearest cover and percentage of bare ground covered with small pebbles or gravel (Table 2). To a lesser degree, percentage of accretion dunes and the number of patches of rocks was positively associated with lizard presence/absence. Habitat variables that influenced P. mcallii occurrence were the number of patches of vegetation and percent bare ground (Table 3). The density of active harvester ant

Table 2. Loadings of habitat variables from the Hotelling's T^2 test based on 31 lizard occurrence locations sampled at Ocotillo Wells State Vehicular Recreation Area and the Acquisition Area, June 1991. Loadings with absolute values ≥ 0.30 are emphasized.

Habitat variable	Loading
HVANT	0.01
NVEG	**0.53**
NSAND	0.11
%DUNE	0.17
%BARE	**0.35**
%GRAV	**-0.28**
NTRAIL	-0.13
MNDIST	-0.27
NROCK	0.12

Table 3. Results of the Hotelling's T^2 test and stepdown analysis on the habitat variables sampled at Ocotillo Wells State Vehicular Recreation Area and the Acquisition Area, June 1991.

Independent Variable	Dependent Variable	Univariate F	df	Stepdown F	df
Lizard	HVANT	0.010	1/29	0.01	1/29
	NVEG	12.503	1/29	14.98*	1/28
	NSAND	0.54	1/29	0.31	1/27
	%DUNE	1.31	1/29	0.23	1/26
	%BARE	5.549	1/29	9.09*	1/25
	%GRAV	3.56	1/29	0.88	1/24
	NTRAIL	0.78	1/29	0.21	1/23
	MNDIST	3.40	1/29	3.96	1/22
	NROCK	0.66	1/29	0.07	1/21

* $p < .02$

mounds reflected a very low positive association in lizard occurrence because it was not significantly different between lizard presence and absence locations (Table 4).

The PCA based on a subset of habitat variables yielded two habitat descriptors (factors) as distinguishing features of variance between lizard and scat locations (Table 5). The first two factors extracted from PCA collectively explained 59.1% of the variation in the habitat feature matrix. Factor 1 accounted for 31.2% of the total variance. It can be interpreted as the mean distance to nearest cover and percent bare ground increase, the proportion of the number of patches of vegetation and percent bare ground covered with small pebbles or gravel decrease. This represents a gradient from areas with bare ground in between sparse cover, to bare areas covered with small pebbles or gravel in between many patches of vegetation. Factor 2 accounted for 27.9% of the total variance. This factor can be interpreted as the number of patches of vegetation and rocks increase, the proportion of bare ground covered with small pebbles or gravel and mean distance to nearest cover decrease. Thus, Factor 2 describes a gradient from areas with much cover by vegetation and rocks to bare sites covered with small pebbles or gravel in between sparse cover.

Adult P. mcallii was found to be associated with patches of bare ground covered with small pebbles or gravel in between sparse cover, while their scats were associated with much cover by vegetation and rocks. T-tests applied to locations as quantitatively characterized by PCA showed Factor 1 was not significant, while Factor 2 was highly significant (Table 6). This result indicated scats were correlated with increasing patches of vegetation and rocks, while P. mcallii were correlated with a greater percentage of bare ground covered with small pebbles or gravel and an increase in the mean distance to nearest cover. If lizard locations differ from scat locations in overall habitat features examined, they should cluster together in different areas of the multivariate space as defined by the first two PCA factors. With an exception of 3 lizard locations, locations are clustered in different portions of the multivariate space (Figure 1). These 3 outlying lizard locations probably represented P. mcallii transitions from one type of location to the other.

Table 4. Univariate Analysis of Variance of active harvester ant mound densities between lizard presence and absence locations.

Source	SS	df	MS	F-Ratio	P
Lizard	0.004	1	0.004	0.010	0.93
Error	12.27	29	0.42		

Table 5. Factor loadings on habitat features extracted from Principal Components Analysis of the subset of habitat variables sampled at Ocotillo Wells State Wells State Vehicular Recreation Area and the Acquisition Area, June 1991. Loadings with absolute values ≥ 0.3 are interpreted.

Variables	Factor I	Factor II
Eigenvalue	1.56	1.40
Percent variance	31.2	27.9
Cumulative % variance	31.2	59.1
MNDIST	**0.72**	**-0.40**
%BARE	**0.71**	0.26
%GRAV	**-0.59**	**-0.59**
NVEG	**-0.41**	**0.76**
NROCK	0.13	**0.50**

Table 6. Results of independent t-test comparisons between lizard and scat locations as quantitatively described by Principal Components Analysis (PCA).

	Lizard (18 plots)		Scat (13 plots)				
Feature	Mean	SD	Mean	SD	T	df	p
PCA Factor I	-0.02	1.04	0.03	0.99	-0.13	29	0.89
PCA Factor II	-0.55	0.83	0.76	0.67	-4.70	29	< 0.000

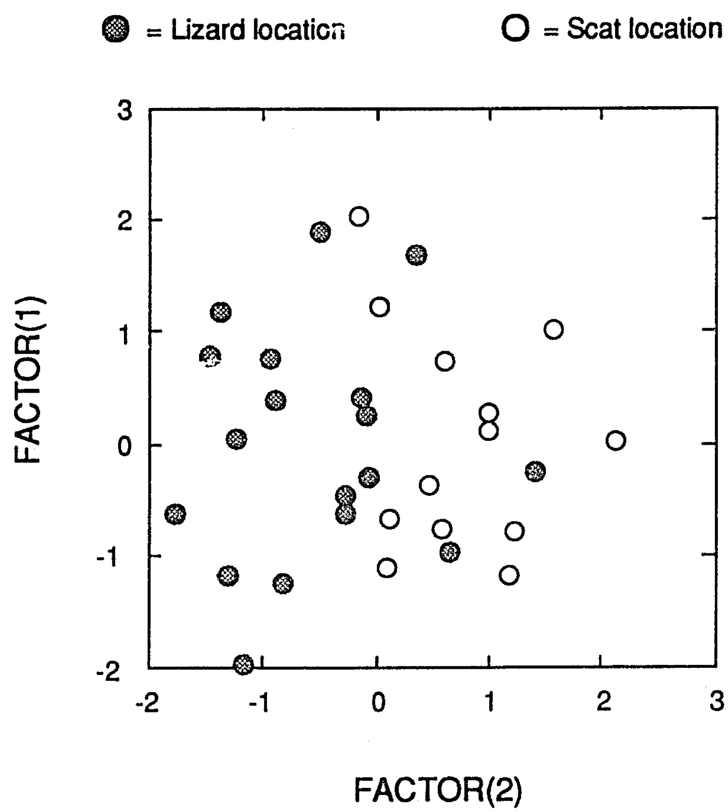

Figure 1. Distribution of lizard and scat locations in the bivariate space as defined by the first two factors of a Principal Components Analysis based on a subset of habitat features.

DISCUSSION

Scat locations were the actual areas where Phrynosoma mcallii defecated. An inverse relationship between lizards and scats may indicate that scats were blown away from the vicinity of a lizard captured/released location by wind action; winds are often strong in the study area. If this was the case, then scats would be located beneath clumps of vegetation and/or broken up in pieces. Because scats counted were observed out in the open and intact (personal observation), wind action cannot account for their locations.

The diversity comparison indicated that both lizard and scat locations offer the same habitat diversity to P. mcallii. Although there may be no habitat diversity differences detectable between lizard and scat locations, P. mcallii utilized both of these habitats because the lizard and/or their scats were found in these locations which would indicate a preference. Perhaps there are other subtle differences not detected by this microhabitat analysis and both lizard and scat locations contain habitat features important to the species that were not taken into account. If this was the case, P. mcallii might not prefer one type of location over the other because each of these contain parts of their habitat requirements.

Cover and substrate affect the distribution of adult P. mcallii within the Ocotillo Wells SVRA and the acquisition area. In addition, the distribution of P. mcallii does not appear to be contingent upon sandy areas. The importance of cover and substrate on the distribution of P. mcallii is not well documented (see introduction; Turner et al., 1980) and may be related to complex combinations of various selective pressures. The importance of cover on the distribution and abundance of desert lizards has been commented on by Degenhardt (1974), Peterson and Whitford (1987), and Shenbrot et al.

(1991). Because P. mcallii shuttles between shade and sun to thermoregulate (Heath, 1965), cover is a likely factor that affects their distribution. Substrate is usually a pronounced factor affecting the distribution of desert lizards (Barbault and Maury, 1981; Ortega-Rubios et al., 1989), and is probably related to aspects of thermoregulation, predator avoidance, and foraging (Gonzalez-Romero et al., 1989; Ortega-Rubios et al., 1989). Sandy substrates did not significantly affect P. mcallii distribution even though they have been noted to occur in sandy areas as Uma sp. (Norris, 1949; Turner et al., 1980; Stebbins, 1985). One likely reason is that in areas where the habitats of the two lizards are allopatric, P. mcallii becomes sympatric with Uma sp., and that P. mcallii has a wider habitat preference than Uma sp. (personal observation).

Significant differences between lizard and scat locations indicate adult P. mcallii utilize different microhabitats at different times of the day. Changes between microhabitat use as a function of daily variation in a desert environment are ecologically and/or physiologically advantageous to lizards (Adolph, 1990a; Castilla and Bauwens, 1991). Although direct data bearing on the microhabitat use hypothesis of P. mcallii are not available at this time, this hypothesis seems likely.

Proximate factors that cause daily shifts in microhabitat use are not fully understood, but may be related to aspects of thermoregulation (Grant and Dunham, 1988; Gonzalez-Romero et al., 1989; Adolph, 1990a; Van Damme et al,. 1990; Castilla and Bauwens, 1991), and predator avoidance (Daniels and Heatwole, 1990; Rocha and Bergallo, 1990). Moreover, a lizard depends strongly upon close substrate adaptations to thermoregulate efficiently and to avoid predators (Sherbrooke and Montanucci, 1988; Gonzalez-Romero et al., 1989). Wone et al. (1991) noted 78% of P. mcallii were captured and released between 0700-0900 hrs., with a marked decrease capture rate thereafter. During this time period, the lizards were basking out in the open (personal observation). Thus, a microhabitat characterized by bare ground covered with small pebbles or gravel located between sparse cover has more open areas for P. mcallii to bask in during the early morning. Further, bare ground covered with small pebbles or gravel provides an excellent backdrop for the cryptic coloration of the species.

Once P. mcallii achieves its preferred body temperature range at about midmorning, it appears to move to a microhabitat with a greater density of vegetation and rocks. Numerous scats located in the densely vegetated microhabitat indicate P. mcallii defecated shortly after the species reached its preferred body temperature range or "normal activity range". Defecation of the blue spiny lizard Sceloporus cyanogenys was most often observed in the morning when basking behavior gave way to perching (Greenberg, 1976, 1977). Perching behavior of S. cyanogenys occurred when the species achieved its preferred body temperature range (Greenberg, 1976). Further, Bradshaw (1986) reported that "most physiological processes in reptiles proceed at optimal rates at temperatures close to the preferred body temperature." Because horned lizards thermoregulate throughout much of the day by shuttling between sun and shade (Heath, 1965), a microhabitat characterized by a greater density of vegetation and rocks will provide more protection from the intense insolation often present from mid morning to late afternoon.

Daily shifts in microhabitat use of P. mcallii may be related to foraging activities (Barbault et al., 1985; Gonzalez-Romero et al., 1989; Ortega-Rubio et al., 1989). Increased patches of vegetation and rocks provide more cover for horned lizards to hide from predators when it typically forages for harvester ants during midmorning and late afternoon (Pianka and Parker, 1975; Munger, 1984a). Although both seed production and germination of desert plants are known to depend on precipitation (Beatley, 1967, 1974), a microhabitat with a greater density of vegetation will produce more seeds for granivorous ants, when compared to a sparsely vegetated one. The species diversity of harvester ants is correlated to seed production (Davidson, 1977). Thus, there will be greater densities of harvester ants within microhabitats characterized by a greater density of vegetation.

The findings reported here have important conservation implications. There has been limited monitoring of P. mcallii distribution and habitat use within the study area based on the relative abundance index of their scats (Bolster and Nicol, 1989; Wone et al., 1991). However, P. mcallii scats alone cannot be used as indicators because findings from this study indicate they merely show where the adult lizard was at some moment during its daily movements. Thus, locations where their scats are found represent only part of their habitat requirements. Moreover, because defecation and decay rates of P. mcallii scats are unknown, attempts to estimate the abundance of the species based on their scats is further biased (Wone et al., 1991).

This study provided quantitative descriptions of habitats that were used by P. mcallii at different times of the day. Thus, the maintenance of appropriate sized areas that are heterogenenous in structural features and substrate should be considered when designing conservation plans for the species within the SVRA and the acquisition area. In addition, these areas need to encompass both the location of lizards and scats. Although the present study elucidates some habitat requirements of P. mcallii relevant to conservation practices, these requirements pertain to adult lizards only. This may confound conservation plans because juvenile P. mcallii may have a different set of habitat requirements than adults. Ontogenetic shifts in habitat use have been documented for numerous other lizard species (Collette, 1961; Hirth, 1963; Jenssen, 1970; Davis and Verbeek, 1972; Laerm, 1974; Scott et al., 1976; Pounds and Jackson, 1983; Stamps, 1983; Adolph, 1990b). In addition, seasonal shifts in habitat use have also been observed (Huey and Pianka, 1977).

Although not conclusive, daily shifts in microhabitat use of adult P. mcallii is a possible explanation for the reduction in capture rate of the species after about 1000 hrs. The reduction in capture rate of P. solare and P. platyrhinos after 1000 hrs. has been commented by Baharav (1971) and Pianka and Parker (1975), respectively. As the day becomes progressively warmer, horned lizards spend increasingly longer periods in the shade (Heath, 1965). By midday these lizards spend most of their time in the shade. During the P. mcallii surveys, most of the lizards captured were nearly stepped on before they were noticed (personal observation). If P. mcallii started to move into a more densely vegetated microhabitat about 0900 hrs., the capture rate would decrease because these cryptically colored lizards would be harder to see.

The present study is the first to document daily shifts in microhabitat use by P. mcallii. However, these shifts in microhabitat use may not be the same for different age classes and seasons. Ontogenetic and seasonal shifts in microhabitat use have been observed in other lizard species (Christian et al., 1983; Paulissen, 1988). Therefore, further research is needed to determine whether microhabitat use varies between habitats (e. g. undisturbed desert environment), season, sex, and age classes. Radiotelemetry has been used to locate transmitter-tagged horned lizards in home range, foraging behavior, and life history studies (Munger, 1984a, 1984b; Allan Muth, pers. comm.). Thus, a detailed study of P. mcallii movements and microhabitat use can be done using radiotelemetry.

Finally, the results from this study showed that scats alone cannot be used as indicators of P. mcallii distribution and habitat use. If meaningful conservation plans are to be developed for this candidate endangered species, more information on its habitat use and requirements is needed.

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